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NOTES ON THE SATYRID BUTTERFLY POPULATIONS OF CORCOVADO NATIONAL PARK, COSTA RICA

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ABSTRACT. Results of a mark-release recapture study of satyrid butterflies at Corcovado National Park, Costa Rica are reported. Seven species were captured in undisturbed primary forest along the Olla Trail. Eleven species, including all but one of the species from the undisturbed habitat, were found in the more heterogeneous habitat along the Rio Claro Trail. Two of the principal forest species, *Pierella luna* Fabricius and *Euptychia arnaea* Fabricius, occur in "viscous" populations (repeated recaptures within a relatively small area), with a predominance of males among captured individuals. The population structure of *Cithaerias* (*Callitaera*) *menander* Drury was extremely "fluid" (no recaptures), with mostly females captured and no behavioral preference for local high points. The other major understory species, *Pierella helvetia incanescens* Godman & Salvin, was not caputred often enough to make any significant biological inferences. Results are discussed with reference to theories of competition, character displacement and ecological disturbance.

The butterfly families Satyridae, Morphidae and Brassolidae have been called a "family cluster" by Young & Muyshondt (1975). They are characterized by monocotyledonous larval food plants (although many morphos feed on legumes), use of non-floral resources (fallen fruit, dung, etc.) as adults (many north-temperate satyrids do feed on flowers) and cryptic, brown to ochre coloration (irridescent blue on the upper wing surface is fairly common among tropical species). Monocots have relatively few secondary compounds, and the generally cryptic color patterns of adults may result from inability to sequester toxic compounds. Larval food preference among monocot feeders does not appear to have "coevolved" along with plant defenses as it has in other groups (Ehrlich & Raven, 1964; Gilbert, 1975). Tropical *Euptychia* species (used here and afterwards in the sense of Weymer, 1924) commonly accept several species of grasses as larval hosts (M. C. Singer, pers. comm.). Young & Muyshondt (1975) report two congeneric species of brassolids which use larval hosts in different families, and in another paper (Young & Muyshondt, 1972) emphasize the importance of factors such as habitat selection in explaining radiations within the genus *Morpho*.

Satyrids, like many groups of new world organisms, reach their greatest diversity in the tropics. Ecology of tropical satyrids has received little attention to date, with the exception of work by Young (1972) and Singer (unpublished). Young (1972) marked individuals of twelve species (including satyrids, brassolids and morphids) at four *Coumarouna oleifera* (Leguminosae) fruit drops at La Selva, Costa Rica. He found little day to day variation in numbers, with the same butterflies returning repeatedly to the same feeding sites. Adult mortality and recruitment were low, and the species composition at the four fruit drops was essentially homogeneous. Most of the species used artificial food when it was offered, but introduction of artificial food did not result in separation of feeding preferences, as would be expected if competition for adult resources were a limiting factor. This study presents basic data on satyrid distributions over a variety of habitats and behavioral comparisons of several species which occupy the same habitat and use the same adult food resources.

METHODS

Corcovado National Park is located on the Osa Peninsula of Costa Rica on the southern Pacific coast. The park headquarters is located in a valley about 1 km from the ocean. The lowlands near headquarters have been used for agriculture in the past, and several habitat types are found, including pasture, second growth and disturbed forest. The surrounding hills are covered with tropical wet forest. This study was carried out in July, which is early in the wet season. Two censusing routes were used, one (the Rio Claro Trail) to sample disturbed habitats and another (the Olla Trail) to sample primary forest. A map of the Sirena (headquarters) area of Corcovado National Park is included in Gilbert et al. (in prep.). The Rio Claro Trail starts just north of headquarters, goes southward up a steep ridge through disturbed primary forest, bears to the north and forks about 0.8 km (one-half mile) from its beginning. The left fork goes to a small landslide clearing and then ends. The right fork goes south along a long ridge, with the Rio Claro to the north. Vegetation along the ridge is very heterogeneous, with *Heliconia* (Musaceae) and *Cecropia* (Moraceae) intermixed with the primary forest species. The trail descends the ridge through an extensive stand of *Heliconia*, goes past a ruined shack in a small clearing, then turns and goes west along the Rio Claro until it reaches the ocean. The forest along the river contains a higher proportion of mesophytic species because of the level topography and consequently increased soil moisture. Total walking distance is about 3.5 km. The Olla Trail goes northeast through slightly disturbed to undisturbed upland forest, after crossing the Rio Camaronal near headquarters. The first 2.5 km were used for study. Both trails were marked with metal tags on tree trunks at intervals of about 50 m.

Censusing was done by walking along the trail and catching as many satyrids as possible. Routes were usually run in the morning between 0730 h and noon. Afternoon rain was very common, and butterfly activity along the trails was somewhat less during the after-

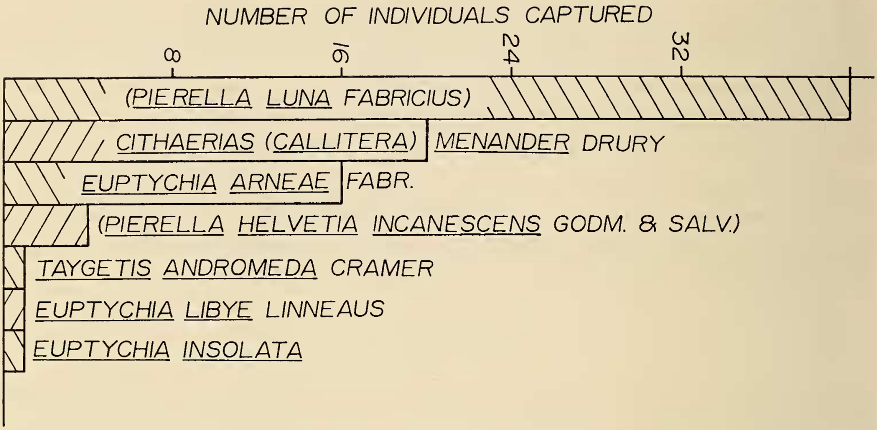

FIG. 1. Total number of butterfly individuals captured along the Olla Trail.

noon. The Rio Claro Trail was sampled on 6, 7, 8, 9, 10, 14, 19, 21, 27 (afternoon) and 28 July 1979, usually starting at the mouth of the river. The Olla Trail was sampled on 11, 12, 13, 15, 18, 20, 25, 27 and 29 July. Capture success was about 60% for most species and somewhat lower for *Pierella helvetia incanescens* Godman & Salvin.

Captured butterflies were marked with a red PILOT ultrafine point pen and then released. (A few butterflies were retained for voucher specimens.) All butterflies were numbered sequentially, regardless of species. The number was written on the undersurface of one hindwing and opposite forewing. Number, sex, species, condition (fresh, worn or intermediate), date, time and location (measured by pacing to the nearest metal marker) were recorded for each capture. Recaptures were released promptly after noting the number and condition.

Horizontal distance between markers was estimated by pacing along the trail, using a compass to determine direction. Capture points were marked on a map, and distances between consecutive capture points for recaptured butterflies were estimated from the map distances. These estimates do not include vertical displacement. Each marker station was rated for local topography ("0" for level ground or local depression, "+" for a slope, "++" for a ridge or hilltop). Abundance of fallen fruit in the vicinity of the marker ("0", none visible; "1", scarce; "2", moderately abundant; "3", abundant) was recorded on 20 July. There was some fluctuation in the abundance of fallen fruit over the course of the study, and no attempt was made to identify fallen fruit to species. Chi-square tests were used to evaluate the significance of observed trends.

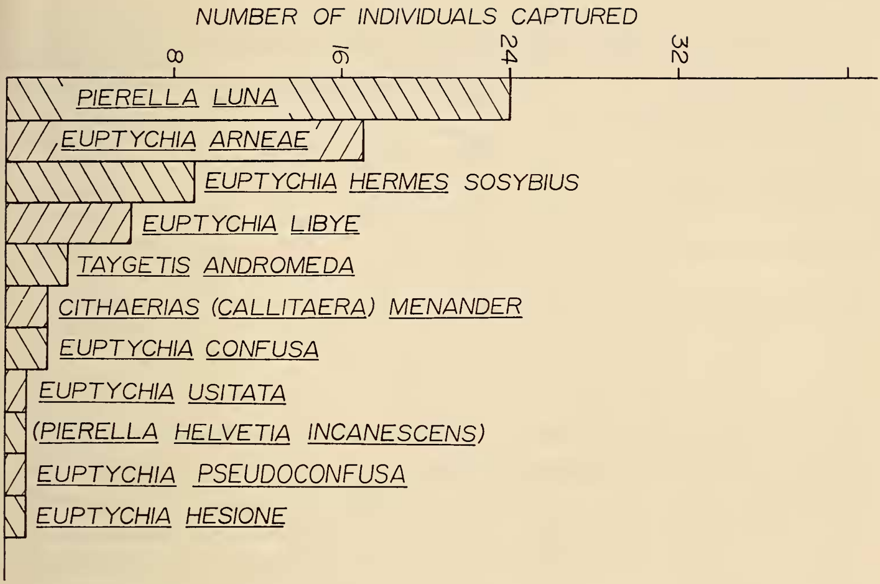

FIG. 2. Total captures along the Rio Claro Trail.

RESULTS

Figs. 1 and 2 show the number of different butterflies of each species captured in each of the two study areas, ranked in order of the number of individuals captured. The Rio Claro Trail fauna is more diverse (11 species, $1/(\Sigma p_i^2) = 4.40$) than that of the Olla Trail (7 species, $1/(\Sigma p_i^2) = 3.03$), in spite of the smaller sample size. Members of the related genera *Euptychia* (Weymer) and *Taygetis* comprise 59% (39 out of 66) of the Rio Claro sample and only 22% (18 out of 82) of the Olla Trail sample. Several species usually found in open or second growth habitat (*Taygetis andromeda* Cramer, *Euptychia hermes* Linnaeus, *Euptychia usitata* Butler, *Euptychia hesione* Sulzer, *Euptychia libye* Linnaeus) were captured in or near the clearing on the Rio Claro Trail. *Cithaerias menander* Drury was much less abundant in the Rio Claro area (n = 2 vs. n = 20).

Table 1 shows basic capture data for the four most common Olla Trail satyrids. *Pierella luna* Fabricius and *Euptychia arnaea* Fabricius were predominantly males. Recaptures were common in both species. One *P. luna* was captured six times within a 5 m radius, while another moved at least 1268 m between four capture points. The longest movement between captures by any *E. arnaea* was 30 m. Most of

TABLE 1. Capture-recapture data on major Olla Trail satyrid species.

		No. of butterflies	No. sampled	No. recaptured	No. of recaptures	Mean recapture distance (S.D.) (m)
Pierella luna	♂	35	0	22	48	73.2 (107.2)
	♀	5	2	0	0	—
Cithaerias menander	♂	6	0	0	0	—
	♀	14	2	0	0	—
Euptychia arnaea	♂	14	0	5	8	7.6 (12.6)
	♀	1	0	0	0	—
Pierella h. incanescens	♂	1	0	0	0	—
	♀	3	1	0	0	—

the *C. menander* captures were females, and there were no recaptures of this species. The biased sex ratios are probably a result of behavioral differences between the sexes. The absence of *C. menander* recaptures indicates a large effective population size, although the density per unit area for *C. menander* and *P. luna* may be roughly comparable.

Table 2 gives the number of male *P. luna* captured (Olla Trail), the number recaptured (second and subsequent captures of the same butterfly on the same day are omitted), and a simple Lincoln index (N = n(C + R)/R, where n is the number of individuals previously marked, N is the estimated population density, C is the number of new captures on that day and R is the number of recaptures) estimate of population number for each day of the study. The mean estimated population size is 41.85, with standard deviation 13.96. By sampling along the trail, I believe I effectively covered an area of about one hectare.

Table 3 shows the number of captures in relation to topography. There were six level stations ("0") covering 367 m of trail, 21 stations on slopes ("+", 1201 m) and 17 stations on ridges or hilltops ("++", 914 m). Expected values were calculated by multiplying the number of total captures (including recaptures) for each species by the pro-

TABLE 2. Number of new captures (C), recaptures (R) and Lincoln-index estimates of population density (N) of *P. luna* males on the Olla Trail.

	Date (July)								
	11	12	13	15	18	20	25	27	29
C	9	6	3	4	7	3	1	1	1
R	0	2	4	3	3	5	7	11	8
N		36.0	26.25	42.0	73.3	46.4	36.6	36.0	38.25

TABLE 3. Total captures (Olla Trail), by topographic position of nearest marker. Expected values in parentheses. See text for further explanation.

	0	+	++	
P. luna	2 (9.31)	41 (42.58)	45 (32.41)	$\chi^2 = 14.26$, df = 2, P < 0.005
C. menander	0 (2.96)	11 (9.68)	9 (7.37)	$\chi^2 = 3.50$, df = 2, P > 0.10
E. arnaea	0 (3.40)	7 (11.13)	16 (8.47)	$\chi^2 = 11.62$, df = 2, P < 0.005
P. h. incanescens	0	0	4	P = 0.0184

portion of trail belonging to that given topographic category. For example, the expected number of *P. luna* captures at level stations is (88)[367/(367 + 1201 + 914)]. *P. luna* and *E. arnaea* both had a significant preference for local high points. *C. menander* captures showed no significant trend. *P. h. incanescens* also seemed to prefer high points, although the number of captures was very small.

Table 4 shows total captures for each species, according to local abundance of fallen fruit on 20 July. Two stations (122 m of trail) had no fruit visible nearby, 26 stations (1378 m) were rated as "1", 11 stations (655 m) were rated as "2" (moderately abundant) and five stations (327 m) were rated as "3". Expected values were calculated by multiplying the total number of captures by the proportion of trail assigned to that rating group. Capture distributions were significantly non-random for all species except *P. h. incanescens*. For the other three species, there was a trend toward higher capture frequencies around high densities of fallen fruit. The trend is less pronounced for *P. luna* than for *C. menander* or *E. arnaea*. Eighteen of the 23 *E. arnaea* captures were within 100 m of a single large fruit drop. The

TABLE 4. Total captures (expected values in parentheses) by abundance of fallen fruit around the nearest marker (Olla Trail).

	Fruit abundance				
	0	1	2	3	
P. luna	2 (4.31)	39 (48.89)	34 (23.21)	13 (11.59)	$\chi^2 = 8.42$, df = 3, P < 0.05
C. menander	0 (0.98)	7 (11.11)	3 (5.28)	10 (2.63)	$\chi^2 = 20.08$, df = 3, P < 0.005
E. arnaea	0 (1.13)	12 (12.78)	1 (6.07)	10 (3.03)	$\chi^2 = 21.45$, df = 3, P < 0.005
P. h. incanescens	0	2	1	1	

TABLE 5. Total captures (Olla Trail) by time of day.

	Time					
	0730–0830	0830–0930	0930–1030	1030–1130	1130–1230	After 1230
P. luna	14	24	26	18	4	2
C. menander	8	5	3	2	1	1
E. arnaea	1	13	5	3	1	0
P. h. incanescens	0	1	1	1	1	0

C. menander Ptures were distributed among several widely separated sites. There was no significant association between topography and abundance of fallen fruit.

Table 5 shows the number of captures by time of day for *P. luna*, *C. menander*, *E. arnaea* and *P. h. incanescens*. *C. menander* were most active early in the morning. *E. arnaea* were most active around 0900 h, and *P. luna* showed a slight peak around 1000 h. Very little time was spent collecting after 1200 h, so the picture presented in Table 5 is incomplete. Wet weather usually depressed activity in late morning or early afternoon, but all four species were seen flying on sunny afternoons.

DISCUSSION AND SUMMARY

Cutting along the Rio Claro Trail has created openings and allowed invasions by successional plant species, such as *Heliconia*. The greater habitat diversity results in greater satyrid diversity, with several *Euptychia* species occurring which are not found in the forest. This result supports recent suggestions of Gilbert (1980) and Huston (1979) that ecological disturbance may increase species diversity.

The behavior of *C. menander* reported here is markedly different from that described by Young (1972). Young reported small, closed demes, with the same individuals returning to the same place day after day. The opposite seems to be true at Corcovado: Different individuals were captured at the same place and time on different days. Young (1972) also found a mid-day peak in activity, with no sightings before 0830 h. Several hypotheses may be proposed as explanations. The habitat at Corcovado is more hilly, so fruit drops might be smaller and less persistent through time. This would generate a more fluid population structure. Repeated movements in the same area might increase chances of predation, although there is no reason to believe this should be more important at Corcovado. A more scattered, ephemeral distribution of larval resources at Corcovado might also result in a more mobile population. Interference competition with *P.*

luna may also play a role. *P. luna* (which is not present at Young's study site) is an aggressively territorial species and often chases conspecifics. The early morning activity peak and mobile flight behavior of *C. menander* would both reduce the chances of being chased by a *P. luna*. Young (1973) reports aggressive patrolling behavior in one of his La Selva species (*Morpho amathonte* Deyrolle). According to Young (1972), *M. amathonte* flies early in the morning at La Selva before *C. menander* becomes active there.

P. luna usually flies low to the ground, often following the contour of the trail for 20 or 30 m. They are extremely cryptic against the background of forest litter: Young individuals resemble wet leaves when at rest, and older butterflies resemble dry leaves. Males will patrol the same area repeatedly, and encounters often result in chasing behavior. Positioning on ridges and hilltops may confer some advantage in mating, as Shields (1967) has reported in several temperate species. According to Scott (1968), "hilltopping" is usually an adaptation to low population densities, but densities of *P. luna* were not especially low during the study. Access to food may also be important. Occasional long flights may reflect searching for a territory with adequate food and few competitors.

E. arnaea is usually encountered in small sunny areas within the forest, with several males present in the same place. Scott (1974) lists several situations which should favor "perching" (as opposed to patrolling) as a mate location strategy, including low population density and patchy resource distribution. *E. arnaea* is less common and more patchily distributed than *P. luna* at Corcovado, so either one could be responsible for the observed behavior. Both predominantly male species (*P. luna* and *E. arnaea*) prefer local high points, while *C. menander*, which flies singly (usually female) or in pairs at Corcovado, doesn't. *Cithaerias* and *Pierella* are placed close together in most classification schemes (Weymer, 1924), even though their behavior in this situation is very dissimilar. Both *C. menander* and *E. arnaea* show slight sexual dimorphism with respect to size (males are smaller) and wing color. *P. luna* males have conspicuous scent patches (androconia) near the upper rear edge of the hindwings.

Previous work by Gilber & Singer (1973) has demonstrated that spatial distribution of resources may affect flight and mating behavior in butterflies. Results presented here indicate that interspecific competition may also have a significant impact. Comparison of behavior of related species in the same area and of single species in different areas, combined with accurate measurement of niche parameters such as food preference and flight time, will be needed to clarify this issue. Detailed descriptions of courtship, mating, oviposition behavior and larval life histories are also necessary.

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